PALAEOBIOGEOGRAPHY OF TETHYS PERMIAN CRINOIDS

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WEBSTER, GARY D., 1998:11:30. Palaeobiogeography of Tethys Permian crinoids. *Proceedings of the Royal Society of Victoria* 110(1/2): 289–308. ISSN 0035-9211.

Tethyan Permian crinoids are recognised in Australia, India, New Zealand, Oman, Pakistan, Sicily, Thailand, Timor, Tunisia and the southern part of the Ural Mountains. The oldest are from the early Sakmarian of Timor and the youngest are from early Wuchiapingian of Western Australia and Timor. Unresolved stratigraphic problems and indiscriminate collecting of the Timor faunas leaves uncertainies about their age.

The palaeogeographic distribution of the crinoid faunas extends from the Southern Ural Mountains in the north (34.6°N,47°E), to New Zealand (73.6°S,146.7°E) in the southeast, to equatorial faunas from Sicily (3.1°N,21.1°E) and Tunisia (1.9°S,17°E) in the westernmost part of Tethys. Most faunas were in the southern and southeastern parts of the Tethys Sea. Australia, India, Oman and New Zealand were located greater than 35°S and were cooler water faunas, whereas all others were warmer water faunas within 35° of the paleoequator.

The most abundant and diverse faunas are reported from Timor (Sakmarian to Wuchiapingian), Australia (late Sakmarian through Artinskian), and the Ural Mountains (late Artinskian). Of the 52 families and 136 genera recognised in Tethyan faunas, 12 families (23%) and 93 genera (68%) are endemic. Poterioerinitid inadunates dominate all faunas. Camerate, inadunate and flexible crinoids are known into the early Wuchiapingian. Major extinction of the Permian crinoids began in the late Wordian when the record ends for 90% of the Permian crinoids.

In Oman, India, Australia, New Zealand and some of Timor faunas were living on a quartz-sand or volcaniclastic substrate. All other Tethyan faunas were living on carbonate or clay substrates. No Tethyan faunas are known to have been living on reefs, except the late Changhsingian reefs with associated crinoid stems of southern China and the Wordian Tunisian fauna.

TWO crinoids discovered in New South Wales (M'Coy 1847; Dana 1847) were the earliest described Permian crinoids from the Tethys. Although additional crinoids were reported from both the eastern and western parts of Australia later in the 1800s and early 1900s (Gregory 1849; Ratte 1885, 1886; Foord 1890; Etheridge 1892, 1903; among others), it was the fantastically rich and diverse Permian crinoid faunas of Timor, discovered in the early 1860s (Beyrich 1862), and described in a series of papers by J. Wanner between 1910 and 1951, that captivated the attention of crinoid workers worldwide. Large collections of the Timor crinoid faunas were made during expeditions led by J. Wanner in 1909 and 1911, G. A. F. Molengraaff in 1910–1911, J. Weber in 1911, H. G. Jonker in 1916 and H. A. Brouwer in 1936 (Schubert 1915; Haniel 1915; Wanner 1926; Brouwer 1942). Specimens collected on these expeditions may be found in museums and universities in Europe and the United States, but most are reposited in Delft and Leiden, The Netherlands. Although Permian crinoids are now known from every continent except Antarctica, none of the other faunas is as diverse nor specimens as abundant as the Timor faunas.

During the past 150 years nearly 65 papers have described crinoid cups and crowns, or recognisable parts thereof, from what are here collectively referred to as the Tethys Permian crinoid faunas. These faunas are recognised on their taxonomic and palaeogeographic relationships. A total of 136 genera (Table 1) and over 400 species (Webster, unpubl. data) have been identified from more than 100 localities in Australia, India, New Zealand, Oman, Pakistan, Sicily, Thailand, Timor, Tunisia and the southern Urals in Russia.

Geochronologic terms used (Fig. 1) are modified from Zhou et al. (1995) and Yugan et al. (1997). Caution is recommended when referring to the faunas of Timor for correlation or age determination as explained in Webster (this vol.).

CRINOID LOCALITIES AND FAUNAL RELATIONSHIPS

Numerous crinoid localities are known in both

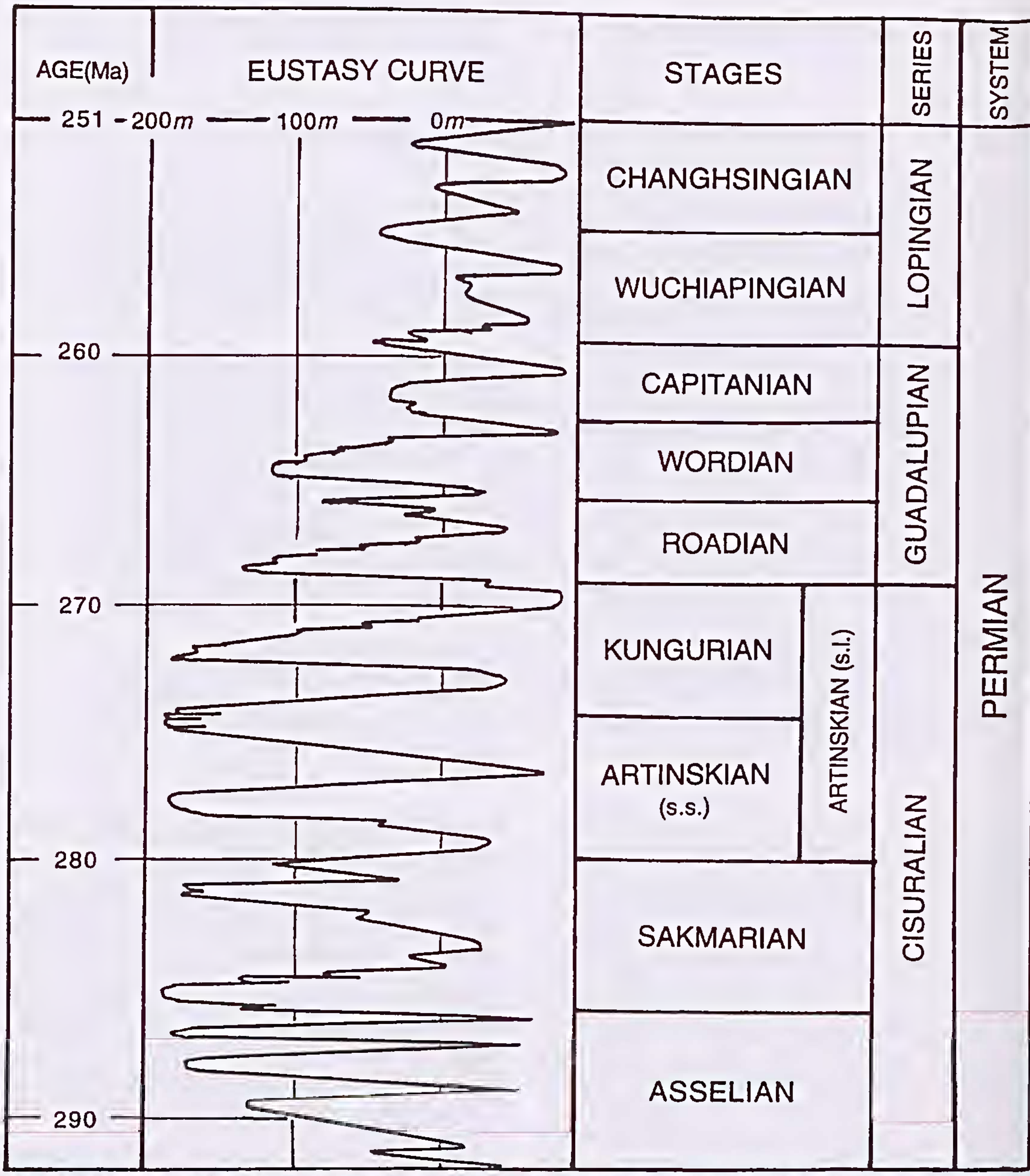

Fig. 1. Permian geochronologic terms and age chart (after Zhou et al. 1995; Yugan et al. 1997); eustasy curve (after Ross & Ross 1994). Note radiometric dates may differ slightly from those of Figs 2–5.

Australia and Timor, and both areas yield specimens of Early and Late Permian age, whereas most other Tethys localities are considered to be of a single age, within either the Early or Late Permian. In a few localities genera found in more than one horizon, but nearly coeval, are herein considered a single fauna for simplicity (e.g. genera occurring in three or four horizons in the latest Sakmarian and earliest Artinskian of southern Thailand are referred to as the Thailand fauna). Stratigraphic and faunal relationships of each area are discussed individually.

Locality	Camerates	Disparids	Inadunates Cyathocrinitids	Poteriocrinitids	Flexibles
Amarassi	1	—	3	4	5 (1)
Basleo	12 (4)	9 (5)	20 (9)	41 (14)	12 (7)
Tae Wai	—	—	1 (1)	2	1
Bitauni	1	1	1	—	—
Somohole	2	—	2 (1)	1	—
Total*	12 (4)	9 (5)	22 (11)	41 (14)	13 (8)

Table 1. Taxonomic distribution of Timor Permian crinoid genera. Numbers in parentheses ( ) are endemics. *Total is different genera, not total numbers from all localities.

Locality	Camerates	Disparids	Inadunates Cyathocrinitids	Poteriocrinitids	Flexibles
Timor	12 (4)	9 (5)	22 (11)	41 (14)	13 (8)
Australia	8 (1)	4 (1)	5 (1)	20 (8)	—
Southern Urals	3	3 (1)	5	11 (3)	3
Sicily	1	1	1	5	1
Tunisia	2 (1)	—	1	3 (1)	2 (2)
Oman	—	—	—	3 (2)	—
Thailand	—	1	—	2	—
Pakistan	—	—	1	1	—
India	—	—	—	1	—
New Zealand	—	—	—	1	—
Total*	17 (11)	13 (9)	27 (17)	64 (43)	15 (13)

Table 2. Taxonomic distribution of Tethyan Permian crinoid genera. Numbers in parentheses ( ) are endemics. *Total is different genera, not total numbers from all localities.

Timor

Problems of the stratigraphy and ages of the Timor crinoids are discussed by Webster (this vol.). In summary, there are 92 reported crinoid localities on Timor (Wanner 1924a, 1924b; among others; Webster, unpubl. comp.). Unfortunately the stratigraphy of most of the Timor localities is uncertain, as noted in early expeditions (Wanner 1931; de Roever 1940). At least five crinoid horizons occur in Timor and they are between Sakmarian and Wuchiapingian in age. The cephalopod based age of each of the 'five' Timor faunas is used herein when referring to these faunas for correlation and taxon affinities. However, it is clearly understood that the stratigraphic problems of the Timor faunas must be resolved before the biostratigraphy and the palaeobiogeography of the Tethyan crinoids can be unquestionably resolved.

Identified crinoid genera from each of the 'five' Timor faunas are given in Appendix 1, cols 1–5. The Permian faunas of Timor include 99 identified crinoid genera, two of which are unclassified. The 97 classified genera are summarised in Table 1. The Basleo faunas are the largest known and include 94 of the 97 genera (97%). Although dominated by the poteriocrinitids, the fauna contains representatives of each of the major groups of Palaeozoic crinoids. The camerates, rapidly waning after the Early Carboniferous, have their greatest Permian diversity in Timor. The flexibles attain their third greatest diversity in the Palaeozoic in Timor. If the Wordian age is correct for all crinoid genera from the Basleo region, then the final extinction of most Palaeozoic crinoids occurred in the Wordian or shortly thereafter, prior to the end of the Permian.

Australia

Australian Permian crinoids range in age from early Sakmarian into early Wuchiapingian (Appendix 1, cols 6, 7). They are dominated by poteriocrinitids and camerates (Table 2) (Teichert 1949, 1954;

Webster 1987, 1990; Webster & Jell 1992) but lack flexibles, with the exception of an unidentified flexible recognised on a disarticulated radial plate (Webster 1987).

In eastern Australia the stratigraphic distribution and descriptions of Permian crinoid genera were documented by Willink (1978, 1979a, 1979b, 1980a, 1980b). The oldest known Australian Permian crinoids are found in the early Sakmarian Darlington Formation of New South Wales. Most eastern Australian faunas are from Artinskian strata, but they range into the late Wordian or possibly early Capitanian. Their primary affinities are with Western Australian faunas and secondarily with Timor.

The stratigraphic distribution of crinoids in Western Australia is well documented with excellent exposures and occurrences of ammonoids at numerous levels throughout the stratigraphic section providing good age control. However, some uncertainty about the age of a few horizons exists. For example, the Callytharra Formation contains late Sakmarian ammonoids at the base, but the fossil-rich upper part, lacking ammonoids, has been considered early Artinskian (Dickins & Shah 1979; Webster 1987; Webster & Jell 1992). Most Western Australia crinoids are of late Sakmarian or Artinskian age. Primary affinities of the Western Australian faunas are with the Basleo faunas of Timor and secondarily with eastern Australia. Taxa from the Cherrabun Member of the Hardman Formation are of early Wuchiapingian age.

Krasnoufimsk, Southern Ural Mountains, Russia

Late Artinskian crinoids from Krasnoufimsk, in the southern part of the Ural Mountains (Appendix 1, col. 8), were described in several papers by Yakovlev (1926, 1927, 1930a, 1937) and Arendt (1968). A strong Tethys character dominates the three camerates, 19 inadunates, and three flexibles in the Krasnoufimsk fauna (Table 2). Of the 25 genera recognised, 15 genera are common with the Basleo fauna, four genera are endemic, four genera are common to the Sosio fauna of Sicily, one genus is common to Western Australia, and one genus is cosmopolitan. Only nine of the 25 genera of the Krasnoufimsk fauna are common to non-Tethyan faunas of Europe and North America and six of these nine are also present in the Basleo fauna. The four genera common to the Sosio fauna are also present in the Basleo fauna and range in age from late Artinskian to Wordian. The late Artinskian age of the Krasnoufimsk fauna may suggest a like age for part of the Basleo fauna.

Sicily

The Wordian Sosio Limestone of Sicily (Appendix 1, col. 9) (Yakovlev 1930b, 1934, 1938; Strimple & Sevastopulo 1982) contains nine crinoid genera (one camerate, seven inadunates, and one flexible) of which six are common to the Basleo fauna (five of these are also common to Krasnoufimsk), two to Tunisia, and one thick-plated basal? circlet, judged to be incorrectly assigned to *Agassizocrinus*?. The Tethyan character dominates this fauna as only two of the genera occur in non-Tethys faunas.

Tunisia

Crinoids from Djebel Tebaga, Tunisia (Appendix 1, col. 10) were described by Valette (1934), Termier & Termier (1949, 1958), Termier et al. (1977) and Lane (1979). The eight genera identified (two camerates, four inadunates, and two flexibles) include four endemic genera, two in common with Sicily, and two in common with the Basleo fauna. This fauna probably reflects a reefal environment as suggested by Lane (1979). The age of the fauna is Wordian, based on cephalopods, to perhaps Capitanian, based on fusulinids (Lane 1979). It may be slightly younger than the Basleo fauna, but is not as young as the Amarassi or Cherrabun faunas.

Oman

Three inadunate crinoids in the latest Sakmarian or earliest Artinskian Ghariff Formation of Oman (Appendix 1, col. 11) (Jell & Willink 1993) include two endemic genera (Table 2) and *Texacrinus*, common to the Early and Late Permian of Western Australia. An undescribed platycrinitid camerate and a *Deltoblastus*, on loan to George Sevastopulo and seen by me, are also from the Ghariff fauna; they support a Tethyan character for the fauna.

Pakistan

Four of the five species of crinoids from the Middle Productus Limestone (=Wargal Formation, in part, of current usage) reported by Waagen (1887) are considered incorrectly assigned to *Cyathocrinus*, later corrected to *Cyathocrinites* (Appendix 1, col. 12). Moore & Plummer (1940) transferred *Cyathocrinus goliathus* to *Ulocrinus*? *goliathus* and Webster (1981) considered *C. indicus* and *C. kattaensis* to belong to an unnamed new genus of inadunates. The fourth species, *Cyathocrinites virgalensis*, is based on disarticulated basal plates and columnals, which may or may not belong to a single species. These four species belong to two or three genera, but not *Cyathocrinites* or *Ulocrinus*. The fifth species originally identified as *Phialocrinus cometa* de Koninck, 1863, is recognised as *Woodocrinus cometa*. As currently identified, these taxa do not show strong Tethyan affinities. Some of these species may belong to *Cibolocrinus* or *Stuartwellercrinus* sensu J. Wanner (1937, 1949). If so, the fauna would show stronger Tethyan relationships. The Wargal Formation was considered basal Tatarian or late Guadalupian by Dickins (1992). Species from the Salt Range described by de Koninck (1863) and Reed (1925) were assigned a Carboniferous age. Both are from the Permian, but may not be coeval with those reported by Waagen (1887).

India

The Tethyan crinoid from the Permian of India (Appendix 1, col. 13) is the inadunate *Calceolispongia*, known from isolated basal plates in central India (Reed 1928; Gerth 1936). This fauna was considered as possibly equivalent to the Callytharra fauna of Western Australia (Dickins & Shah 1979). The *Calceolispongia* plates correspond most closely to Artinskian forms of Western Australia, but Archbold (1982) considered the Umaria Beds middle Sakmarian.

Thailand

Permian crinoids from Thailand are from the late Sakmarian Phuket Group and the Artinskian part of the Rat Buri Limestone (Appendix 1, col. 14). At least two, and probably three, horizons have yielded crinoids in the Rat Buri Limestone (Webster & Jell 1993). Of the three inadunate genera identified from the Rat Buri Limestone, all are known in Western Australia, Timor, or Krasnoufimsk, as well as non-Tethyan faunas of North America.

New Zealand

A partial specimen, identified as *Tribrachiocrinus*? sp. (*sic.*), and an unidentified set of arms were reported, but not illustrated, by Waterhouse & Vella (1965) from Kungurian clastic strata. The specimens are mentioned for palaeobiogeographic purposes.

TETHYAN ENDEMICS

A total of 136 genera of crinoids assigned to 52 families are recognised in Permian strata of the Tethys (Tables 1, 2; Appendix 1). This does not include specimens described or illustrated that were not assigned to a genus, nor does it include specimens questionably assigned to a genus, if the genus is also questionably recognised. The total does not include three genera listed in Table 1: (1) *Jonkerocrinus*, which was based on an anal sac that is probably referable to *Cadocrinus*; (2) *Teratocrinus*, which is based on disarticulated basal plates (probably belonging to *Calceolispongia*) and anal sac plates (probably belonging to *Timorechinus*); and (3) *Ammonicrinus*, which is based on columnals, probably belonging to *Calycocrinus*. Endemics make up 68%, 93 of the 136 genera, of the Tethys crinoids (Table 3). Thus, endemics make up slightly over ⅔ of the Tethyan genera, but range from zero to 40% at the family level. Slightly over 23%, 12 of 52 families, are endemic. Among flexible crinoids, 13 of 15 genera (87%) are endemic, but only 2 (40%) of 5 familes, to which the 15 genera are assigned, are endemic. This is the highest percentage of endemics at the genus and family level of the Tethyan crinoids.

	Families	Genera
Camerates	6	17
Endemics	1 (17%)	11 (65%)
Disparids	5	13
Endemics	1 (20%)	9 (69%)
Cyathocrinitids	5	27
Endemics	0	18 (67%)
Poteriocrinitids	31	64
Endemics	8 (26%)	42 (66%)
Flexibles	5	15
Endemics	2 (40%)	13 (87%)
Total	52	136
Endemics total	12 (23%)	93 (68%)

Table 3. Number of families and genera of major taxonomic groups of Tethyan Permian crinoids.

With the exception of Thailand and possibly Pakistan, Tethyan endemic genera are known from each of the localities discussed above. In general, Tethyan endemic genera are advanced forms within the class or order to which they are classified. Sixteen endemic genera are restricted to the cooler water environments of Australia, New Zealand and Oman, while most endemics are found in the warmer water environments of Timor, Tunisia and Krasnoufimsk.

The non-endemic taxa may be divided into three groups. (1) Long-ranging cosmopolitan taxa, such as *Platycrinites, Actinocrinites, Kallimorphocrinus, Litocrinus, Synbathocrinus* and *Cyathocrinites.* These taxa are judged to have had wide ecological tolerances, allowing them to adapt to the cooler water environments of Australia, as well as occupy normal niches in the warmer water environments. (2) Range extension genera, or holdovers (such as *Pleurocrinus* and *Cydonocrinus*), that are not known outside the Tethys in the Permian, but are well known outside the Tethys in Carboniferous strata. Some of the range extension taxa are questionable generic assignments, such as *Agassizocrinus*?, *Gissocrinus*? and *Dichocrinus*?. Most of these taxa will probably be reassigned to new genera with additional study, and become part of the Tethyan endemics. (3) Non-endemics, such as *Stuartwellercrinus, Synyphocrinus* and *Neozeacrinus.* These taxa are known from Permian deposits of North America or Europe, but are not recognised as truly cosmopolitan. The second and third groups of non-endemics provide insights (as well as posing problems) concerning the worldwide palaeobiogeographic distribution patterns and dispersal routes for the Permian crinoids.

Crinoid genera are generally short lived. Relatively few taxa have stratigraphic ranges exceeding one or two series (Lane & Webster 1980). Many genera are known from one locality and from one bedding surface. Tethyan crinoids are no exception to these generalities. Of the 136 genera identified, only 40 (29%) are known from more than one stratigraphic horizon within the Tethys (Table 1). Most of these are Tethyan endemics from Australia and Timor or the long-ranging cosmopolitan genera. Recognition of the short stratigraphic range of most crinoid taxa enhances their biostratigraphic value and questions the age of the Basleo faunas of Timor.

PALAEOBIOGEOGRAPHY

During the Permian, the Tethyan faunas were distributed around the Tethys Sea (Figs 2–5). The palaeolatitude and palaeolongitude of individual localities (Appendix 2) reflects the wide distribution of the crinoid faunas within the Tethys. The earliest known fauna is from Somohole, Timor, 62.1°S,102.4°E (incorrectly located on Fig. 3). The fauna from Krasnoufimsk was the northern-most fauna at 34.6°N,47°E (Fig. 3) and New Zealand the southern- and eastern-most at 73.6°S,146.7°E (Fig. 3). Faunas from Sicily (3.1°N,21.1°E) and Tunisia (1.9°S,17°E) were in the western-most part of the Tethys close to the Equator (Fig. 4). Faunas from Oman (40.3°S,53.7°E), Pakistan (33.7°S, 54.8°E), India (52°S,53.6°E), Timor (33.3°S, 102.4°E), Australia (various localities from 39–69°S,83.4–148.8°E) and Thailand (28.5°S,98.4°E) were in the southern and southeastern part of the Tethys Sea (Figs 2–5). Eastern Australian faunas were in marginal basins bordering Panthalassa. No Permian faunas have been reported from the central-eastern and northeastern parts of the Tethys Sea. The Oman, India, Australia and New Zealand faunas were located greater than 35°S and cooler water faunas, whereas all other faunas were north of 35°S and warmer water faunas.

The localities (Figs 2–5) are dated within the stages for the individual map. Although some localities on each map (e.g. localities 10, 20–23, Fig. 3) are coeval, based on the faunas and or associated invertebrates, most are of differing ages, within a few million years. Localities listed on more than one map such as locality 10, Callytharra Formation, range from late Sakmarian into early Artinskian and are therefore plotted on Figs 2 and 3.

Most Permian crinoid localities have been interpreted as shallow shelf environments (Figs 2–5). However, a few localites on Figs 2–5 are shown in other environmental settings. Most of the apparent inconsistency of plot and environmental setting is the result of scale (locality 5, Fig. 3), perspective (locality 4, Fig. 3), and possibly the age difference between that of the locality and the average age used for the map (locality 15, Fig. 3). Radiometric ages (Fig. 1) followed by Zhou et al. (1995) differ from those of the Ziegler maps (Figs 2–5).

Some slight revisions of the boundaries between environments or interpretations of the environment of the site of deposition may also be needed for a few localities. For example localities 1 and 18 (Fig. 2) are plotted in a lowland environment rather than a marine environment, and neither locality has been reworked. One other inconsistency is the plot of localty 31 (Fig. 5). This is the Amarassi, Timor locality, currently considered to be of Wuchiapingian age and plotted well south of the Timor block. This suggests that Timor did not move to the north until after the Wuchiapingian or that the age interpretation of the Amarassi locality is incorrect. As noted by Webster (this vol.), the Amarassi crinoid fauna is at least of Wuchiapingian age, based on cephalopods, and may be younger than the cephalopods.

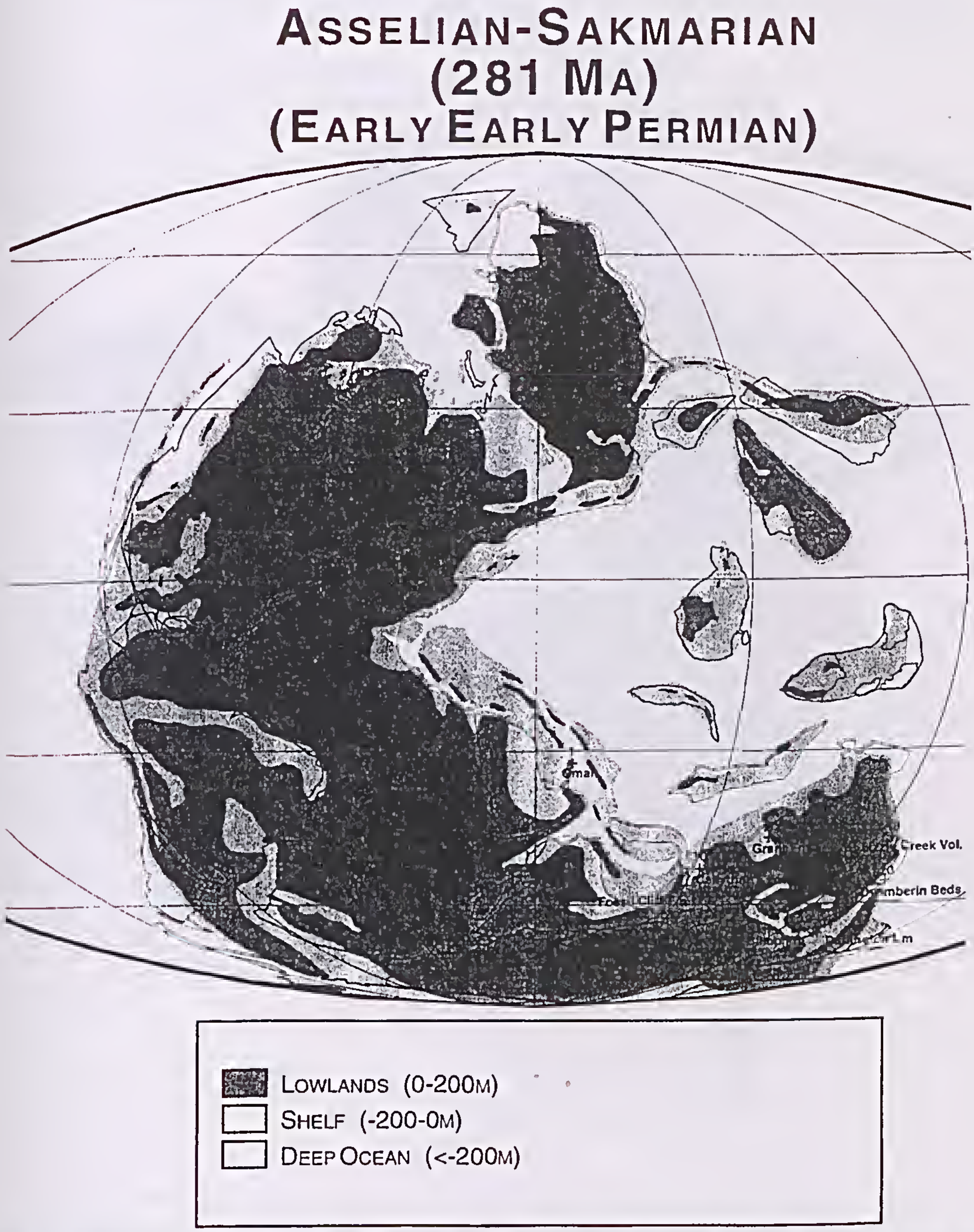

Fig. 2. Palaeogeographic map showing distribution of Asselian–Sakmarian crinoid localities in Tethys. Based on the maps of Ziegler et al. (1997). Palaeolatitude and palaeolongitude co-ordinates given in Appendix 2.

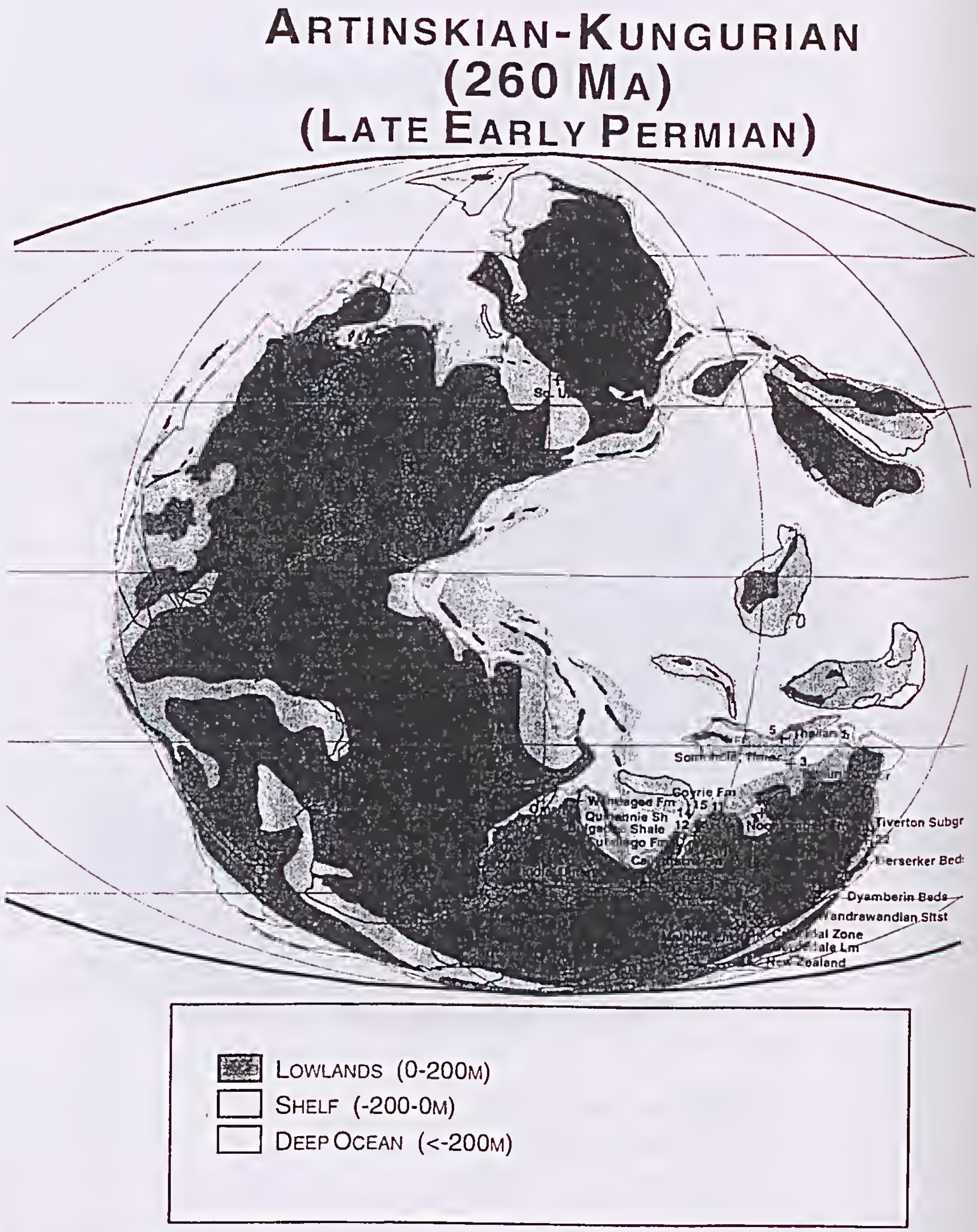

Fig. 3. Palaeogeographic map showing distribution of Artinskian–Kungurian crinoid localities in Tethys. Localities with age of Sakmarian–Artinskian repeated on Figs 2 and 3. Based on the maps of Ziegler et al. (1997). Palaeolatitude and palaeolongitude co-ordinates given in Appendix 2.

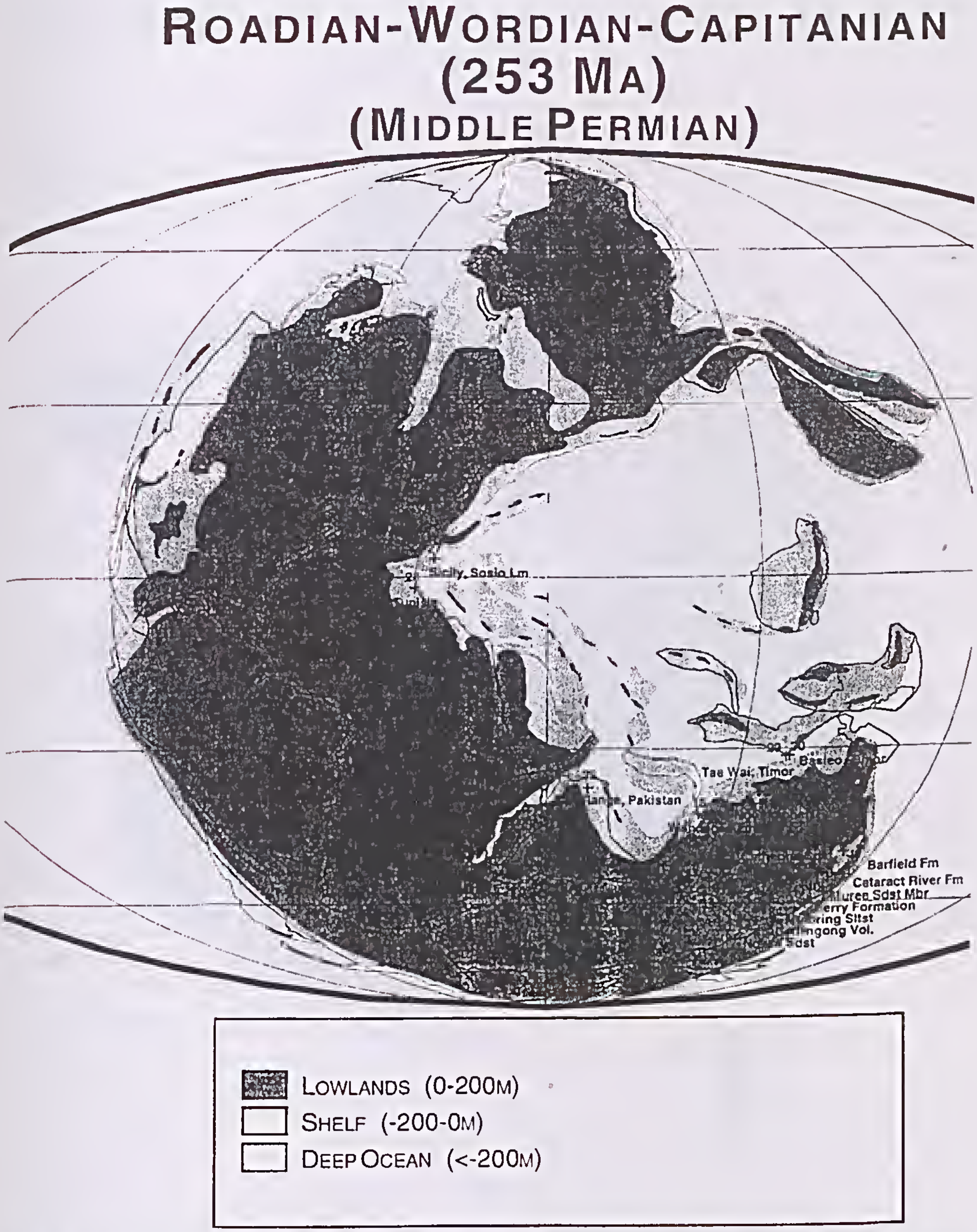

Fig. 4. Palaeogeographic map showing distribution of Roadian–Wordian–Capitanian crinoid localities in Tethys. Based on the maps of Ziegler et al. (1997). Palaeolatitude and palaeolongitude co-ordinates given in Appendix 2.

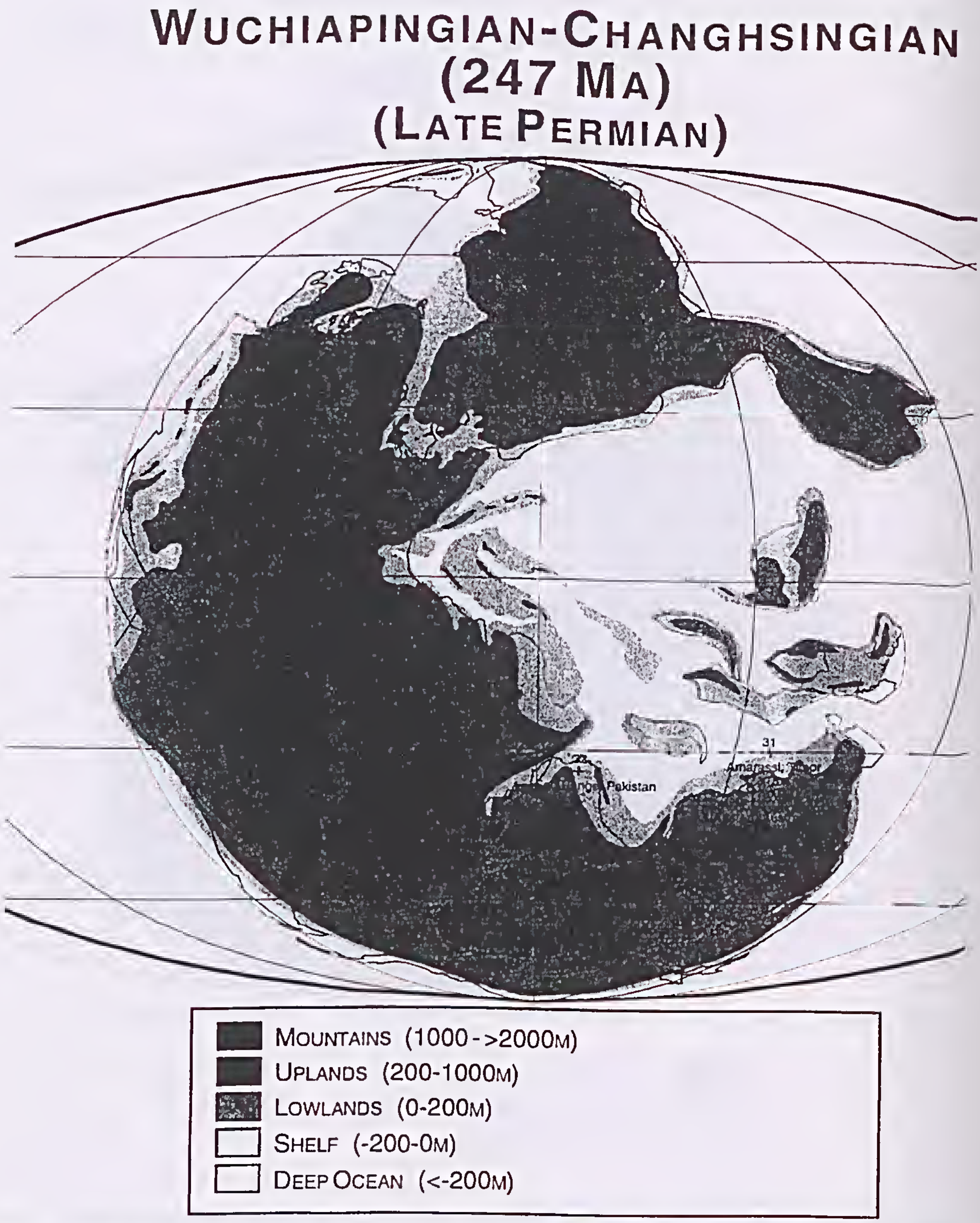

Fig. 5. Palaeogeographic map showing distribution of Wuchiapingian–Changhsingian crinoid localities in Tethys. Based on the maps of Zicgler et al. (1997). Palacolatitudc and palaeolongitude co-ordinates given in Appendix 2.

The early Sakmarian to Wuchiapingian age span of the Tethyan Permian crinoids includes nine of the eustasy highstand cycles (Fig. 1) as proposed by Ross & Ross (1994). Crinoid faunas dated by cephalopods occurring in the same stratigraphic unit, or on stratigraphic position with respect to underlying and overlying units dated by cephalopods or other invertebrates, may be correlated with these cycles. The phase position within the Ross and Ross cycles of most of the Tethyan faunas remains to be determined. The most diverse and abundant faunas are from the Artinskian and Wordian cycles.

Tethyan crinoid faunas of the Sakmarian are of low diversity and tend to lack taxa common to one another. Faunas of the late Sakmarian and early Artinskian are the third most diverse known in the Tethys (Figs 2, 3). They occur in Oman, several formations in Western Australia, several formations in eastern Australia, India and Thailand. Except for Thailand, they are all cooler water faunas. Faunas are dominated by poteriocrinitids (nine genera, in nine families) followed in decreasing numbers by camerates (five genera, in four families), disparids (four genera, among three families), and cyathocrinitids (three genera in three familiies). Flexibles have not been identified in these faunas. Calceolispongiids radiated during this interval and are present in Australia and India. Latest Sakmarian and early Artinskian coeval faunas from widely separated localities within the marginal basins of Australia have a few genera in common. This implies that the basins were interconnected or oceanic currents were such that crinoid larvae could be dispersed around the Australian block.

The middle and late Artinskian faunas are the second most abundant in the Tethys and occur in the southern Urals, Timor (Bitauni) and eastern and Western Australia (Fig. 3). Faunas are dominated by poteriocrinitids (19 genera, 15 families) and contain six genera of camerates (two families), two disparid genera (two families), seven cyathocrinitid genera (five families) and two flexible genera (two families). They contain the oldest identified Permian flexible crinoids in the Tethys. These faunas developed during the middle and late Artinskian (s.l.) cycles of Ross & Ross (1994).

The occurrence of common genera and some species between Western Australia Artinskian localities (Callytharra and Wandagee) with the Timor localities of Bitauni (Artinskian) and Basleo (Wordian) shows a much greater degree of communication between these regions than that between eastern and Western Australia. This also provides strong support for questioning the Wordian age of all Basleo faunas.

The number of Tethyan endemics, common to Timor and Krasnoufimsk, shows that oceanic circulation patterns connected the southeastern and north central parts of the Tethys Sea during the Artinskian. Because the ages of the Bitauni and Basleo faunas are uncertain the place of origin and dispersal patterns of taxa common to Timor and Krasnoufimsk or Timor and Australia are speculative at this time. The discovery of Permian crinoid faunas in terranes of the central-eastern and northeastern parts of the Tethys could help resolve the evolutionary patterns and biogeographic distribution within the Tethys.

Wordian faunas are present in Timor (Tae Wai and Basleo), Sicily, Tunisia, Pakistan and eastern Australia (Fig. 4). The Basleo fauna is the most diverse and abundant Tethyan fauna known. The cooler water faunas of eastern Australia only have two genera in common with Basleo. Wordian faunas were dominated by poteriocrinitids (51 genera, 31 families) and in decreasing numbers, contain cyathocrinitids (21 genera, five families), camerates (16 genera, five families), flexibles (15 genera, five families) and disparids (10 genera, five families). If the Basleo fauna is of one age, this was the peak occurrence of all major crinoid groups in the Permian of the Tethys and 90% of these taxa became extinct shortly after this occurrence.

Two localities, Amarassi, Timor and the Millyit Range of Western Australia contain the youngest described Permian crinoids (Fig. 5). These faunas are dominated by poteriocrinitids (six genera, five families) and flexibles (four genera, four families) and also contains two camerate genera (two families) and one cyathocrinitid (one family). The Wuchiapingian faunas contain the few survivors of the massive crinoidal extinction that began in the Wordian. The faunas were developed in the early Wuchiapingian cycle of Ross & Ross (1994).

ENVIRONMENTS

Palaeozoic crinoids are normally found in limestones, shales or marls that are lacking in quartz grains (Lane & Webster 1980). Many of the Australian crinoids (Tethyan endemics and non-endemics) were living on a quartz sand substrate environment, such as in the Cundlego and Wandagee Formations of Western Australia and the Catherine and Nowra Sandstones of eastern Australia, and volcanic-rich substrates, such as the Lizzie Creek and Gerringong volcanics of eastern Australia. These forms include the calceolispongiids with their distinctly coiled arms, when in the feeding posture (Willink 1979b). Most of the carbonate- and clay-dominated substrate environments of Australia and Oman contain quartz and other non-carbonate sand-size grains. The Australian and Oman deposits are considered cooler water deposits (Dickins 1992; Jell & Willink 1993). The cool water and sand rich substrates are unusual living environments for Palaeozoic crinoids, although warm water quartz sandstone environments yielding numerous crinoids are also known in the Early Devonian Colbenzian of Germany (Schmidt 1934, 1942) and the Silurian and Early Devonian of Victoria (P. A. Jell, pers. comm.). All non-Australian Tethyan crinoids, except those reported from volcaniclastics and a conglomerate in the Basleo area (J. Wanner 1924b), the arenaceous carbonates of Oman and the clastics of New Zealand are from carbonate or clay substrates, and all non-Australian, Indian, New Zealand and Omani localities are considered shallow shelf, warm-water environments.

Although crinoids are often associated with reefs, none of the Tethyan faunas summarised herein are found in reefal deposits. The Tunisian fauna is from claystones near reefs and Lane (1979) suggested that the crinoids may have been living on the reef flanks and were transported short distances to the burial site. The Timor faunas were considered reefal associated by Audley-Charles (1965, 1968), but non-reefal by Hamilton (1980) and Archbold & Bird (1989). Crinoid stems, but no cups or crowns, in late Changhsingian reef deposits of southern China were reported by Flügel & Reinhardt (1989).

CONCLUSIONS

The palaeogeographic distribution of Permian crinoid faunas within the Tethyan Sea extends from the southern Urals in the north to New Zealand. Near equatorial faunas from Sicily and Tunisia were in the westernmost part of the Tethys. Faunas from Oman, Pakistan, India, Timor, Western Australia and Thailand were in the southern and southeastern part of the Tethys Sea. Eastern Australian faunas bordered Panthalassa.

The oldest faunas reported, based on cups and crowns, are from early Sakmarian strata of Timor and the youngest are from early Wuchiapingian of Western Australia and Timor. The most abundant and diverse faunas are reported from Timor (Wordian?), Australia (late Sakmarian through Artinskian), and the Urals (late Artinskian).

Of the 52 families and 136 genera recognised in the Tethyan faunas, 12 families (23%) and 93 genera (68%) are endemic. Poteriocrinitid inadunates dominate all faunas. Camerate, inadunate (disparids, cyathocrinitids and poteriocrinitids), and flexible crinoids are present through the Wordian and, except for the absence of the disparids, into the early Wuchiapingian. Poteriocrinitids (6 of 13 genera) and flexibles (5 of 13 genera) dominate the early Wuchiapingian faunas. The major extinction of Permian crinoids began in the late Wordian when the record ends for 90% of them.

The Omani, Indian, Australian and New Zealand faunas, located south of 35°S were cooler water faunas, whereas all others were warmer water faunas. The Omani, Australian, New Zealand and part of the Timorese faunas were living on a quartz sand or volcaniclastic substrate. All other Tethyan faunas lived on carbonate or clay substrates. No Tethyan faunas are known to have been living on reefs, except the late Changhsingian reefs with associated crinoid stems of southern China and the Wordian Tunisian fauna.

The unresolved stratigraphic problems and indiscriminate collecting of the Timorese faunas leave uncertainies about their age. Gaps in the data base for palaeobiogeographic patterns of the Tethys are particularly obvious in the lack of information from its central-eastern and northeastern parts.

ACKNOWLEDGEMENTS

Palaeogeographic maps were provided by A. M. Ziegler of the Palaeogeographic Atlas Project at the University of Chicago, based on the maps of Ziegler et al. (1997). The hospitality of Eric Groessens and use of the library of the Belgian Geological Survey, as well as office space and use of facilities of the Geological Institute of the University of Amsterdam, Queensland Museum and Geology Department at Trinity College, Dublin are gratefully acknowledged. Washington State University provided professional leave during which this study was initiated. Reviews by P. A. Jell, C. G. Maples and G. Shi are gratefully acknowledged.

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Families, Genera	1	2	3	4	5	6	7	8	9	10	11	12	13	14
CAMERATES														
Paragaricocrinidae														
*Paragaricocrinus**									w	w				
*Tunisiacrinus**										w				
*Wannerocrinus**				w										
Actinocrinitidae														
Actinocrinites				w		s/a								
Coelocrinidae														
cf. *Dorycrinus*						s/a								
Dichocrinidae														
Dichocrinus?						a	a-c							
Camptocrinus				w				a						
Camptocrinus?							a							
*Neocamptocrinus**						s-wu	s-w							
Neocamptocrinus?							s							
*Neodichocrinus**				w										
*Stomiocrinus**				w		a?r		a						
Eutelecrinidae*														
*Eutelecrinus**	s			w	wu									
*Metaeutelecrinus**				w										
*Paraeutelecrinus**				w										
*Plesiocrinus**				w										
Platycrinitidae														
*Neoplatycrinus**	s			w		s-a								
Platycrinites		a		w		s/a		a						
Pleurocrinus				w										
DISPARIDS														
Calceocrinidae														
*Epihalysiocrinus**								a						
Allagecrinidae														
Kallimorphocrinus								a						a
Litocrinus						s/a								
*Metallagecrinus**				w				a	w					
*Wrightocrinus**				w		s/a								
Catillocrinidae														
Allocatillocrinus				w										
*Isocatillocrinus**				w										
*Neocatillocrinus**				w										
*Notiocatillocrinus**						s/a	s/a							
*Paracatillocrinus**				w										
*Xenocatillocrinus**				w										
Synbathocrinidae														
Synbathocrinus				w		s/a								
Paradoxocrinidae*														
*Paradoxocrinus**		a		w										
CYATHOCRINITIDS														
Cyathocrinitidae														
Cyathocrinites												w?c		
*Ceratocrinus**				w										
Gissocrinus?							r							
*Occiducrinus**						a?r								
Barycrinidae														
Barycrinus?						s/a								
Codiacrinidae														
Abrachiocrinus				w										
*Asymetrocrinus**				w										

Appendix 1 continued next page (see legend on page 307)

Families, Genera	I	2	3	4	5	6	7	8	9	I0	11	12	I3	14
CYATHOCRINITIDS (*continued*)														
Codiacrinidae (*continued*)														
Cranocrinus				w										
Cydonocrinus				w		s/a								
*Embryocrinus**				w										
*Hypocrinus**				w	wu					w				
Tenagocrinus				w										
*Bolbocrinus**				w	wu			a						
*Nereocrinus**				w				a						
*Thetidicrinus**				w										
*Prochoidiocrinus**				w										
Sycocrinitidae														
*Allosycocrinus**				w										
*Metasycocrinus**		a		w	wu									
*Monobrachiocrinus**				w				a	w					
*Parasycocrinus**			r/w											
Streblocrinidae														
*Atremacrinus**				w										
Coenocystis	s			w										
*Hemistreptacron**				w				a						
Lampadosocrinus						s/a								
Neolageniocrinus	s													
*Pilidiocrinus**				w										
*Acariaiocrinus**				w				a						
POTERIOCRINITIDS														
Poteriocrinitidae														
Poteriocrinites				w			a							
Scytalocrinidae														
*Omanicrinus**											s/a			
*Roemerocrinus**				w										
Woodocrinus												w?c		
Corythocrinidae														
*Campbellicrinus**											s/a			
Aphelecrinidae														
Cosmetocrinus?						s/a								
Spaniocrinidae														
Spaniocrinus				w										
Stuartwellercrinus				w						w				
Mollocrinidae														
*Mollocrinus**	s			w										
*Hemimollocrinus**								a						
Strongylocrinus				w				a						
Indocrinidae														
*Indocrinus**				w										
*Contignatocrinus**				w										
*Eoindocrinus**						a?r								
*Pumilindocrinus**				w										
Rimosindocrinus				w										
*Proindocrinus**								a						
Pachylocrinidae														
*Depaocrinus**				w										
Malaiocrinus				w										
Agassizocrinidae														
Agassizocrinus?									w					
Ampelocrinidae														
*Meganotocrinus**							r-w							
*Spheniscocrinus**				w		a								

Appendix 1 continued next page (see legend on page 307)

Families, Genera	1	2	3	4	5	6	7	8	9	10	11	12	13	14
POTERIOCRINITIDS *(continued)*														
Sundacrinidae*														
*Sundacrinus**				w				a						
*Basleocrinus**				w				a	w					
*Laccocrinus**				w										
*Parindocrinus**				w										
Tribrachyocrinidae*														
*Tribrachyocrinus**							a-w							
Anobasicrinidae														
Synyphocrinus				w										
Trimerocrinidae*														
*Trimerocrinus**				w				a						
Decadocrinidae														
*Trautscholdicrinus**					a									
Cromyocrinidae														
*Hemiindocrinus**								a						
*Minilyacrinus**						s/a								
Ulocrinus				w				a						
Cadocrinidae*														
*Cadocrinus**				w	a									
Graphiocrinidae														
Graphiocrinus				w	a			a	w			w?c		
Graphiocrinus?				w										
*Coenocrinus**										w				
Contocrinus												w?c		
*Permiocrinus**				w										
*Tapinocrinus**				w		s?r								
Paradelocrinidae														
*Lopadiocrinus**				w										
Catacrinidae														
Delocrinus				w	wu			a						
Delocrinus?				w										
*Paraplasocrinus**				w	wu									
Laudonocrinidae														
Bathronocrinus								a						
*Tetrabrachiocrinus**									w	w				
Stachyocrinidae*														
*Stachyocrinus**				w					w					
*Parastachyocrinus**				w										
Apographiocrinidae														
Apographiocrinus				w		s/a								a
*Paragraphiocrinus**				w										
Texacrinidae														
Texacrinus						s-wu					s/a			
Galateacrinidae														
Galateacrinus						s/a								
Stellarocrinidae														
*Anechocrinus**						a								
Cymbiocrinidae														
Cymbiocrinus						wu								a
Oklahomacrinus				w										
Zeacrinitidae														
Neozeacrinus				w										
Timorocidaridae*														
*Timorocidaris**			r/w	w										
Timorechinidae														
*Timorechinus**				w		s/a								

Appendix 1 continued next page (see legend on page 307)

Families, Genera	1	2	3	4	5	6	7	8	9	10	11	12	13	14
POTERIOCRINITIDS (*continued*)														
Timorechinidae (*continued*)														
*Benthocrinus**				w										
*Notiocrinus**				w										
*Parabursacrinus**				w		s/a								
*Prolobocrinus**				w										
Calceolispongiidae*														
*Calceolispongia**				w		s?r	s-wu						a	
*Jimbacrinus**						a								
Jimbacrinus?							a							
Family uncertain*														
*Nowracrinus**							w							
*Tasmanocrinus**							s							
FLEXIBLES														
Mespilocrinidae														
Cibolocrinus				w				a	w					
*Loxocrinus**				w										
*Petrocrinus**				w	wu									
*Strobocrinus**										w				
*Syntomocrinus**				w	wu									
*Trinalicrinus**										w				
Calycocrinidae														
Calycocrinus			r/w	w	wu			a						
*Plagiocrinus**				w										
Ammonicrinus (col)								a						
Prophyllocrinidae*														
*Prophyllocrinus**				w	wu									
*Ancistrocrinus**				w										
*Peripterocrinus**				w										
*Proapsidocrinus**				w										
Palaeoholopodidae*														
*Palaeoholopus**					wu									
*Permobrachypus**				w										
Dactylocrinidae														
*Rumphiocrinus**				w										
UNCLASSIFIED														
*Jonkerocrinus**				w										
*Teratocrinus**				w										

Appendix 1. Families and genera of Permian crinoids from various localities in Tethys. *Key to localities 1–14:* 1, Somohole, Timor—early Sakmarian; 2, Bitauni, Timor—Artinskian; 3, Tae Wei, Timor—late Roadian or early Wordian (=basal part of Basleo); 4, Basleo, Timor—Wordian; 5, Amarassi, Timor—early Wuchiapingian; 6, Western Australia—late Sakmarian to early Wuchiapingian; 7, Eastern Australia—early Sakmarian to Wordian; 8, Krasnoufimsk—late Artinskian; 9, Sosio—Wordian; 10, Tunisia—late Wordian; 11, Oman—Sakmarian–Artinskian; 12, Pakistan—Wordian or Capitanian; 13, India—Artinskian; 14, Thailand—Artinskian. For Australia: s, Sakmarian; a, Artinskian; r, Roadian; w, Wordian; c, Capitanian; wu, Wuchiapingian; known ranges given as s-w, etc.; uncertain ranges given as s?r, etc.; uncertain age at stage boundaries given as s/a, etc. Asterisk (*) indicates a non-Tethyan report of the taxon is considered a misidentification and the taxon is considered endemic to Tethys. (col), generic identification based on columnals.

1.	Oman	late Sakmarian	—58.205	37.709
1.	Oman	early Artinskian	—66.709	36.018
2.	Somohole, Timor,	late Asselian/early Sakmarian	—33.225	102.437
3.	Bitauni, Timor	Artinskian	—33.323	102.414
4.	New Zealand	Artinskian	—73.634	146.722
5.	Thailand	Artinskian	—28.522	98.41
6.	Krasnoufimsk, Southern Urals	Artinskian	34.622	46.966
7.	India, Umaria	Artinskian	—51.955	53.641
8.	Grant Formation, Western Australia	Sakmarian	—46.219	106.371
9.	Fossil Cliff Formation, Western Australia	Sakmarian	—55.893	90.572
10.	Callytharra Formation, Western Australia	late Sakmarian	—46.933	85.206
10.	Callytharra Formation, Western Australia	early Artinskian	—52.458	91.73
11.	Coyrie Formation, Western Australia	Artinskian	—44.303	85.269
12.	Bulgadoo Shale, Western Australia	Artinskian	—45.238	85.637
13.	Cundlego Formation, Western Australia	Artinskian	—46.138	85.17
14.	Quinannie Shale, Western Australia	Artinskian	—44.995	85.071
15.	Wandagee Formation, Western Australia	Artinskian	—42.123	83.422
15.	Wandagee Formation, Western Australia	Roadian	—44.871	84.995
16.	Noonkanbah Formation, Western Australia	Artinskian	—40.204	97.884
16.	Noonkanbah Formation, Western Australia	Roadian	—42.409	99.892
17.	Darlington Limestone, Tasmania	Sakmarian	—66.803	150.768
18.	Lizzie Creek Volcanics, Queensland	Sakmarian	—46.358	138.739
19.	Billop Formation, Tasmania	Sakmarian	—66.674	148.991
20.	Dyamberin Beds, New South Wales	Sakmarian	—55.323	148.811
20.	Dyamberin Beds, New South Wales	Artinskian	—57.45	137.508
21.	Tiverton Subgroup, Queensland	Artinskian	—46.652	130.858
22.	Berserker Beds, Queensland	Artinskian	—49.168	134.154
23.	Crinioidal Zone, Tasmania	Artinskian	—68.652	131.47
24.	Berriedale Limestone, Tasmania	Artinskian	—69.07	129.877
25.	Wandrawandian Siltstone, New South Wales	Artinskian	—61.472	134.654
26.	Malbina Formation, Tasmania	Artinskian	—69.057	131.104
27.	Sicily, Sosio Limestone	Wordian	3.092	21.134
28.	Tunisia	Wordian	—1.899	17.01
29.	Tae Wai, Timor	early Wordian	—31.385	100.182
30.	Basleo, Timor	Wordian	—31.239	100.94
31.	Amarassi, Timor	Wuchiapingian	—29.9	97.878
32.	Salt Range, Pakistan	Wordian	—37.026	54.836
32.	Salt Range, Pakistan	Wuchiapingian	—33.7	54.662
33.	Cherrabun Member, Western Australia	Wuchiapingian	—39.075	97.514
34.	Nowra Sandstone, New South Wales	Wordian	—60.343	129.119
35.	Cataract River Formation, New South Wales	Wordian	—54.308	133.395
36.	Muree Sandstone Member, New South Wales	Wordian	—57.982	131.094
37.	Catherine Sandstone, Queensland	Wordian	—49.514	126.012
38.	Barfield Formation, Queensland	Wordian	—50.645	129.6
39.	Berry Formation, New South Wales	Wordian	—59.531	128.709
40.	Mulbring Siltstone, New South Wales	Wordian	—59.456	129.697
41.	Gerringong Volcanics, New South Wales	Wordian	—59.452	129.534

Appendix 2. Palaeolatitude and palaeolongitude of Tethyan Permian crinoid localities. Locality followed by stage, palaeolatitude, palaeolongitude. South palaeolatitudes indicated by —; all palaeolongitudes east. Locality numbers correspond to localities plotted on Figs 2–5.